
Primary Production in Flowing Waters

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ABSTRACT

Respiration, photosynthetic production, and diffusion interact to produce the daily curve of oxygen change in a segment of flowing water. Conversely, the observed curves of oxygen in streams can be used to calculate the component rates of production, respiration, and diffusion. New production values obtained with these analyses of oxygen curves from various sources, as well as a few previously existing estimates of primary production, indicate a generally higher rate of production in flowing waters than in other types of aquatic environments.

The ratio of total primary production to total community respiration is used to classify communities quantitatively according to their predominantly heterotrophic or autotrophic characteristics. Longitudinal succession within a stream tends to modify the ratio towards unity from higher values for autotrophic and from lower values for heterotrophic communities. The behavior of this ratio is described for the annual cycle in a stream, for the sequence of pollution recovery, and for diverse types of communities.

INTRODUCTION

To the casual eye the biota of flowing waters is rich. Coral reefs, river rapids, tidal channels, and the lush plant beds of calcareous streams seem to be full of life. In the polluted Illinois River, almost unbelievable concentrations of bottom organisms have been found. How are such communities supported? What is the magnitude of primary production in comparison to other communities? How does the dominating current-flow relate to other energy-flows through the communities?

A large literature exists on the limnology of streams and the biology of flowing sea waters, but apparently studies on community function have rarely been oriented to obtain information on primary production (exceptions: Nusbaum and Miller 1952, Sargent and Austin 1949, 1954; Odum and Odum 1955, Purdy as quoted by Phelps 1944). This is very peculiar because the continual mixing makes *in situ* measure-

ments of production very simple in flowing water. The task here, therefore, is to re-evaluate some of the extensive information on flowing waters in terms of productivity and community respiration especially by using diurnal gas curves and the upstream-downstream method of measuring community metabolism. A summary will then be made of the production and respiration of flowing communities relative to succession, velocity of current, and the classification of communities.

THEORETICAL CONSIDERATION OF DAILY PROCESSES OF OXYGEN METABOLISM IN FLOWING WATERS

Consider a stretch of flowing water delimited by two stations, one upstream from the other. During the usual daily cycle four main processes affect the oxygen and carbon-dioxide concentrations of water flowing between the stations. Although the discussion here is presented in terms of oxygen, it should be understood that carbon dioxide behaves similarly but with reversed sign.

(1) There is a release of oxygen into the water as a result of photosynthetic primary production during the day by both benthic plants and phytoplankton.

(2) There is an uptake of oxygen from the water as a result of the respiration of benthic

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organisms, planktonic organisms, and sometimes chemical oxidation.

(3) There is an exchange of oxygen with the air in a direction depending on the saturation gradient.

(4) There may be an influx of oxygen with accrual of ground water and surface drainage along the stretch. In most of the examples discussed here, accrual is assumed to be negligible relative to the other influences.

These processes between stations may be quantitatively summarized on an area basis (i.e., g/m²/hr) as follows:

$$Q = P - R + D_{in} + A \quad (1)$$

Rate of change of dissolved oxygen per area	Rate of gross primary production per area	Rate of respiration per area	Rate of oxygen uptake by diffusion per area	Rate of drainage accrual
Q	P	R	D_{in}	A

Note that capital letters have been used for these quantities that are defined on an area basis.

By dividing through by the depth in meters (z), the relationships are expressed in concentration-units (i.e., g/m³/hr). Small letters have been used for these quantities which are defined on a volume basis.

$$q = p - r + d_{in} + a = \frac{Q}{z} \quad (2)$$

The usual diurnal (24 hours) course of change for the component processes is given in Figure 1 for a hypothetical flowing system without accrual, which is both oversaturated and undersaturated with oxygen relative to the atmosphere and which has a balance of production and respiration. The photosynthesis-curve has the same shape as the incident light with a morning and afternoon symmetry as shown in Figure 1 for a clear day unmodified by cloud patterns.

If the plankton and biochemical oxygen-demand in the inflowing water remains fairly constant as assumed for the case in Figure 1, then respiration remains relatively constant. Whether plant respiration is depressed during photosynthesis or not is still an unsettled question since evidence is conflicting (Rabinowitch 1951, Whitting-

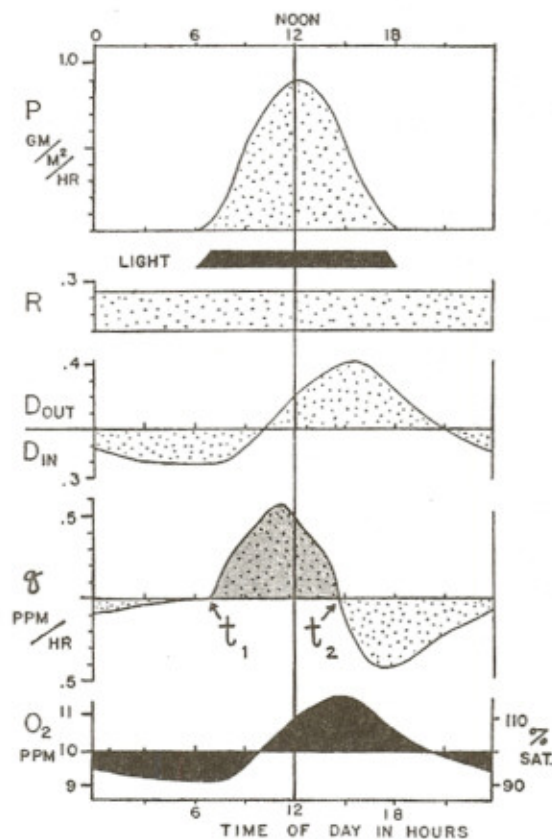


FIG. 1. Component processes in the oxygen metabolism of a section of a hypothetical stream during the course of a cloudless day. Production (P), respiration (R), and diffusion (D) are given on an areal basis. The combined effect of these rate processes for a stream 1 meter deep is given in ppm/hr (q). In the lowermost curve are given the actual oxygen values that would result in a stream with a long homogeneous community. The diffusion curve is linearly proportional to the oxygen concentration curve. The shaded area delimited by t_1 and t_2 is used in Equation (5) to obtain an approximate production estimate uncorrected for diffusion.

ham 1955). In strongly polluted waters with very low oxygen concentrations there may be a diurnal increase in respiratory oxidation during the day due to the formation of photosynthetic oxygen, where at night there is no oxygen. Respiration was found to be dependent upon oxygen tension below 1 ppm for sewage by Pomeroy (1938) and for marine waters by ZoBell (1940). Jackson and McFadden (1954) found an increase in community respiration during the day in lake waters. Until more is known about these and other diurnal effects, it may

be simplest here to continue to assume constant community respiration day and night. This assumption will not apply to flows a short distance below pollution outfall, where the volume of pollution discharge itself is frequently in diurnal cycle so as to cause minimum conditions of oxygen during the day (Schmassmann 1951, Calvert 1932, Mohlman *et al.* 1931).

Ordinarily the accrual of water is small and without daily variation. This is the case in Figure 1 where zero accrual is assumed.

Two recent reviews (Haney 1954, Ammon 1954) summarized knowledge on gaseous transfer into water. The rate of diffusion depends on the degree of saturation of the inflowing water.

$$D = KS = zkS \quad (3)$$

where D is the diffusion rate per area, S is the saturation deficit between water and air, z the depth, K the gas transfer coefficient defined on an area basis (i.e., g/m²/hr for 0% saturation) and k the gas transfer coefficient defined on a volume basis (i.e., g/m³/hr for 0% saturation). The diffusion-curve sketched in Figure 1 was drawn for the case where the inflowing water had a similar history to the water preceding it because of similar conditions upstream. In this case an accumulation of oxygen develops in the water as production exceeds respiration during the morning so that diffusion into the water is replaced by diffusion out as the water becomes supersaturated. During the course of the day the other factors affecting diffusion rate such as depth, velocity, and bottom character tend to remain constant for the section of flow. Stream flows with large temperature ranges and changes in stratification-tendency may be exceptions.

When each of the component rates (P , R , D) given on an area basis are summed as in Equation (1), the total rate of change of oxygen is found for the zone between the two stations on an area basis. If this sum (Q) is divided by the mean depth (z) the rate of change of oxygen concentration is obtained (q), as in Figure 1 for a 1-meter deep flow.

From this rate-of-change curve of oxygen one may construct the curve of oxygen concentration by adding successive hours of change to the oxygen concentration at each hour. Thus, beginning with simple assumptions a diurnal oxygen curve for a stream was constructed (Fig. 1) to illustrate some of the known workings of stream communities. The oxygen curve obtained is typical of the curves observed by authors whose work was examined (see Table 2, also Cerny 1948, Wiken 1936). A morning maximum in the rate-of-change curve and an afternoon maximum in the oxygen-concentration curve are typical. Maximum rate of oxygen decrease occurs after sunset. Minimum oxygen concentration and minimum rates of change occur in the predawn hours. In the next paragraphs the procedure of reversing this analysis is described so that primary production may be estimated from observed oxygen curves.

MEASUREMENT OF METABOLISM IN STREAMS

Measurement of gross primary production

The light-dark bottle method for measuring gross primary production of the community (defined as the sum of the net plant production and community respiration during the daytime) is seldom applicable in flowing waters because much of the community is benthic and heterogeneous rather than planktonic. Furthermore, any measurement made without the normal turbulent flow may be questioned on grounds that production is a function of current flow. The upstream-downstream measurement of oxygen, carbon-dioxide, and other properties is apparently the chief method available for the study of metabolism of flowing water communities.

If the area under the upstream-downstream rate-of-change graph (q in Fig. 1) above a horizontal line drawn through the predawn point is measured, a first approximation to daily, gross primary production is obtained in concentration units (ppm/day). By this procedure one subtracts the accrual, respiration, and diffusion of the predawn hours from the rest of the curve so that these predawn values were representative of the entire day. Where the

change in oxygen concentration during 24 hours is small, so that diffusion is not markedly different between day and night, this approximation will give production values close to but always less than the actual production values. Therefore, the area under a rate-of-change curve of oxygen q (Fig. 1) expressed in ppm/day multiplied by the mean depth between stations (z in m) gives the gross production per area in $g/m^2/day$ (P).

The following is an alternative calculation where the oxygen change is expressed as the difference between stations rather than as the change per hour. The area under a curve of oxygen change between two stations (Δc) expressed in ppm-hours, multiplied by the discharge in m^3/hr (F) and divided by the area between stations in m^2 (X) also gives the gross primary production per day (P).

These conversions may be summarized as follows:

$$P_{day} = z \int_{t_1}^{t_2} (q - q_1) dt \quad (4)$$

$$= \frac{F}{X} \int_{t_1}^{t_2} (\Delta c - \Delta c_1) dt$$

where t_1 is sunrise and t_2 is the time in the evening when q or Δc returns to its value at sunrise q_1 or Δc_1 respectively.

Or as measured in practice:

$$P_{day} = (z)(\text{area under diurnal } q \text{ curve}) \quad (5)$$

$$= \frac{F}{X} (\text{area under diurnal } \Delta c \text{ curve})$$

These areas are hatched in Figures 1, 2, and 3.

The first of the calculation methods is used in the dye spot example for the marine turtle grass (Table 2) and in the analysis of single-station oxygen curves from the literature. The second of the calculation procedures is used in the Silver Springs example.

These simple methods without diffusion-corrections were used by Sargent and Austin (1949, 1954) in coral reef work at Rongelap where deviations from saturation were small relative to the total production.

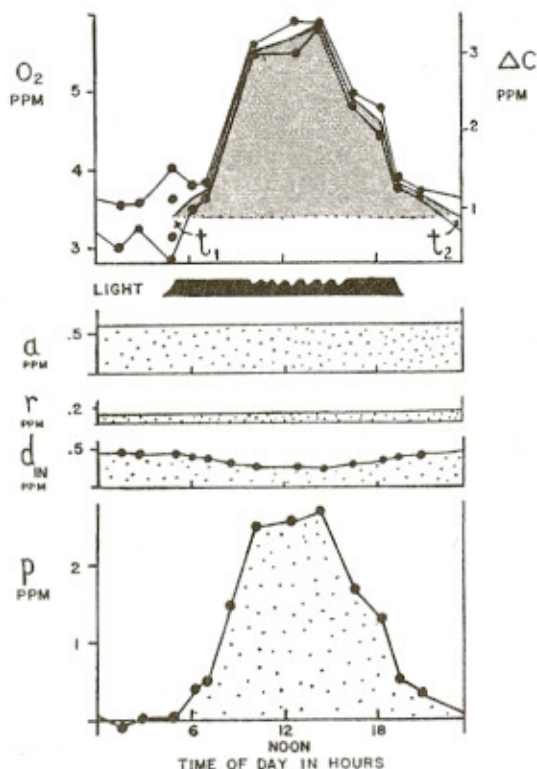


FIG. 2. Component processes in ppm in the daily oxygen metabolism in the upper $\frac{3}{4}$ -mile zone of Silver Springs, Florida, March 23-24, 1954. In the upper graph duplicate oxygen analyses $\frac{3}{4}$ mile downstream from the outflow boil are expressed in ppm on the left ordinate. The ordinate on the right indicates the oxygen change (Δc) relative to the constant boil value of 2.50 ppm. The accrual (a) due to addition of more oxygenated water from side springs, respiration (r) as estimated with black belljars, and the diffusion in (d) as estimated from the gas transfer coefficient and the saturation deficit are given next. In the lower curve the production in ppm is computed by separating accrual, respiration, and diffusion from the observed oxygen change in the $\frac{3}{4}$ -mile zone. The area under the lower curve expressed in ppm-hrs may be converted into daily production as indicated in Equation (5). The shaded area in the upper curve delimited by t_1 and t_2 is used in Equation (5) to obtain an approximate estimate of production uncorrected for diffusion.

It should be noted that the magnitude of diurnal change in ppm oxygen concentration gives no indication of the metabolic rates per area unless depth and velocity or discharge and area between stations are known. Small oxygen changes in deep or rapid streams may indicate larger production values than do larger oxygen changes of oxygen in shallow streams.

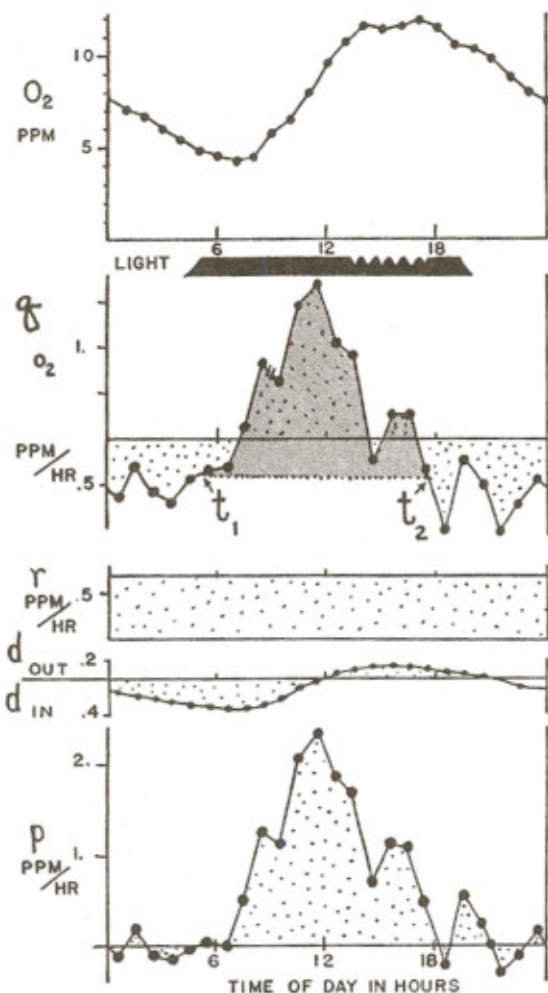


FIG. 3. Component processes in ppm/hr in the daily oxygen metabolism of the River Lark, England, calculated by the single-curve method from data given by Butcher, Pentelow, and Woodley (1930). In the upper curve is given the observed diurnal (24-hr) oxygen curve. From this is calculated the rate of change per hour in ppm/hr (q). Respiration (r), diffusion (d), and production (p) on a ppm-basis are calculated as indicated in the text on the assumption that the stream is homogeneous. The shaded area delimited by t_1 and t_2 is used in Equation (5) to determine the approximate production uncorrected for diffusion.

As considered so far these calculations of gross primary production do not consider diurnal variations in respiration, accrual, and diffusion. Since diffusion ordinarily is the main process which fluctuates diurnally, the success and reliability of the upstream-downstream method is dependent upon the accuracy of corrections for diurnal diffusion-change.

Measurement of diffusion

Especially where differences in rate of diffusion between night and day are large, such as in the diagrammatic example in Figure 2, it is necessary to estimate the change in diffusion due to the daily change in saturation deficit. If a coefficient of gas-transfer (K) is available or can be obtained for the stream section in question, it may be used to apply a correction for each hour of the day, as in Figures 2 and 3 according to the saturation deficit for each hour.

In Table 1 are given various estimates of K for oxygen transfer in flux units. Values for still water with mostly molecular diffusion are about $0.03 \text{ g/m}^2/\text{hr}/0.2 \text{ atm}$. Values for bubbles and droplets as in waterfalls are as high as $34 \text{ g/m}^2/\text{hr}/0.2 \text{ atm}$. The values for flowing waters are in between depending upon the rate at which the surface film is dispersed downward due to turbulent mixing.

The following procedures can be used to measure the gas transfer coefficient in flowing waters:

(a) The gas transfer coefficient may be obtained from two measurements of oxygen content of the water, one after sunset and one just before sunrise.

According to the relationships in equations (2) and (3) before sunrise:

$$q_m = \frac{KS_m}{z} - r \quad (6)$$

where S_m is the predawn saturation deficit and q_m is the rate change of oxygen concentration in the morning. After sunset:

$$q_e = \frac{KS_e}{z} - r \quad (7)$$

where S_e is the evening saturation deficit and q_e is the rate of change of oxygen concentration in the evening.

Subtracting these expressions leads to:

$$K = \frac{z(q_m - q_e)}{S_m - S_e} \quad (8)$$

The gas transfer coefficient can be readily obtained from diurnal oxygen curves by

TABLE 1. *Coefficients of gas transfer for oxygen*

Water type, Source of data	Velocity m/sec	Depth m	Temp. °C	K g/m ² /hr at 0% saturation
Still water				
(Hutchinson, Becker, quoted by Haney, 1954)	0.0	—	20-25	.034
(Adenay, quoted by Kehr 1938)	0.0	—	—	0.03-0.08
Moving water				
Stirred water (quoted by Haney 1954)	—	—	25	0.09-0.74
Shallow circulating trough (Streeter, Wright, and Kehr 1936)	0.01	0.1	0-10	0.037
	0.01	0.1	10-20	0.043
	0.01	0.1	20-30	0.047
	0.013	0.1	12	0.12
	0.070	0.1	17	0.52
	0.119	0.1	14	1.12
	0.20	0.1	13	3.8
Sewage in circulating trough (Kehr 1938)	0.05	0.45	25-26	0.38
	0.15	0.45	25-26	1.5
Stream and ponds (Imhoff and Mahr 1932)	—	—	—	0.08
New York Harbor (Gould 1921)	tidal	—	—	0.23
Tank with a wave machine (Borst, quoted by Phelps 1944)	—	1.8	—	0.31
Sea Surface (Redfield 1948)				
Summer	—	—	12-20	1.1
Winter	—	—	3-7	5.2
Silver River, Florida, July 21, 1955 (Odum)				
Subtraction-of-respiration method	0.21	2.77	23	0.92
Dye-measured-turnover method	0.21	2.77	23	1.00
Green Cove Springs, Florida (Odum) From carbon-dioxide by respiratory-quotient method	0.3	0.23	24	0.55
Small rivers, diurnal oxygen curve analyses in Table 2	—	0.5-3.	—	0.6-4.3
Ohio River below Cincinnati (Velz 1939)	0.05-0.09	4.8	15-25	1.5-5.0
Bubbles and drops (K given per area of drop or bubble)				
Air bubble (Krogh, quoted by Redfield 1948)	—	—	37	13.1
Air bubbles (Ippen, Adenay, Spuler, and Schwab, quoted by Haney 1954)	—	—	20-25	2.8-28.
Water drops (Whitman, quoted by Haney 1954)	—	—	24	22-34.

substitution of measured values in Equation (8).

The rapid production of gases in some cases produces local extreme supersaturations so that bubbles break to the surface without going into solution even in undersaturated waters. Measurements by trapping bubbles in funnel devices showed about 1.5% of the production or 0.3 g/m²/day loss during the daylight hours in Silver Springs. The effect is more important in shallower streams. Even though the rate is partly a function of the saturation deficit, it ceases as an oxygen-loss mechanism at night. Thus, diffusion coefficients determined at night may fail to include this effect. In shallow supersaturated waters this loss leads to underestimation.

(b) If some estimate of the time required for vertical mixing and dispersion of the

surface film is available, the coefficient of diffusion may be computed on theoretical grounds (Phelps 1944, after Black and Phelps 1911). In Silver Springs fluorescein dye was observed from under water with a face mask. The yellow surface film was readily observed to become dispersed vertically in about 1 minute. The calculated gas transfer constant was similar to the inferred value from balance sheet calculations (Table 1).

(c) If a respiration value has been obtained for a stream and if accurate is negligible, the diffusion rate for a known saturation deficit may be obtained by subtracting the respiration from the upstream-downstream change at night. For example, belljar measurements were used to obtain an estimate of respiration in Silver Springs. The diffusion was then calculated (Table 1).

(d) If the diffusion rate is found for one gas (i.e. CO_2) the diffusion rate for another gas may be related as their molecular diffusion coefficients. When transfer coefficients are expressed in $\text{g}/\text{m}^2/\text{hr}/\text{atmosphere}$ saturation-deficit, similar values are found for both gases.

(e) If river slope, velocity, and depth are known, some idea of K may be obtained by using empirical equations based on observations on the Ohio River (Phelps 1944, Streeter and Phelps 1925).

(f) In a section of a river without accrual the difference between gross primary production and respiration, expressed in organic matter, is the organic matter synthesized in this section. $P-R$ is readily measured by upstream-downstream organic matter measurements. Substitution in Equation (1) permits the calculation of the diffusion. This method assumes that sedimentation is balanced by erosion, as in the middle sections of many rivers.

(g) Lacking other means a value may be selected from Table 1 for similar conditions of depth and turbulence.

Measurement of community respiration

Where community respiration is to be measured, the following procedures are available:

(a) Black belljars over typical bottom-substrates and black bottles in the water may be combined to obtain respiration rates. In many streams the black bottle respiration-rate differs from the stream respiration due to differences in bacteria, turbulence, oxygen conditions, and benthic communities. Similar difficulties arise with attempts to anticipate the natural black bottle measurements with BOD tests of pollution effluents.

(b) During darkness, the diffusion may be subtracted from the observed rate of change to obtain the respiration in ppm. The ppm/hr respiration multiplied by the depth in meters gives the respiration per area per time in $\text{g}/\text{m}^2/\text{hr}$. If during darkness there is a time of saturation with respect to the atmosphere, such as occurs after sunset in Figure 1, the upstream-downstream change is equal to the respiration providing the accrual is negligible.

(c) If one gas (i.e. CO_2) is nearly at saturation, and its respiration component can thus be obtained at night, the respiration of the other gas (i.e. O_2) may be obtained assuming a respiratory quotient characteristic of the stream or arbitrarily 0.8 as an approximation.

The methods suggested here for measurement of diffusion, respiration, and photosynthesis are demonstrated in subsequent paragraphs with three examples representing three important, frequently occurring cases.

An example of production measurement in constant inflow situations

Silver Springs, Florida, is an example of chemostatically regulated inflow. Since there is no diurnal change in the upstream station (the boil outflow), the downstream concentration curve is readily converted into an upstream-downstream rate of change curve by subtracting the upstream value from each downstream value and dividing by the time of flow to the downstream station. In Figure 2 is shown the oxygen concentration curve, upstream-downstream change curve, and component respiration, accrual, and production curves based on detailed work presented elsewhere (Odum 1954). The accrual is large and the zone is always undersaturated. Respiration was measured by belljar measurements of the benthic communities, and diffusion estimated as indicated in Table 1. Possible errors in this method were cited previously.

Other flows with fairly constant inflow without much diurnal oxygen variation are found downstream from large waterfalls, in ground water flows, and downstream from surf. The Rongelap and Eniwetok coral reef studies include measurements under situations of relatively constant inflow (Sargent and Austin 1949, 1954; Odum and Odum 1955).

Production measurements by the difference between upstream and downstream diurnal curves

For the usual complex case where no simplifying assumptions may be made about the inflowing water, complete curves should be taken at two stations. Upstream-down-

stream changes were used in the coral reef studies of Sargent and Austin (1949, 1954) and Odum and Odum (1955). The upstream and downstream curves in Schmassmann (1951) are examples of data to which this analysis might be applied if information on depth and flow rate were available. The upstream curve can be subtracted from the downstream curve after shifting the upstream curve to the left by a time period corresponding to the time required for the flow to pass from the first to the second station. Unfortunately, most of the diurnal oxygen and carbon-dioxide curves in the literature are from single stations.

An example of production measurement by single curve analysis

Where a curve for only one station is available, but an assumption of stream homogeneity above the zone of measurement is reasonable, the curve for rate of change may be obtained from a single diurnal oxygen graph. With this procedure one assumes that the incoming water had had the same diurnal history as the water just preceding. In other words the whole stream is experiencing a simultaneous rise and fall of oxygen. In a stream where this assumption applies perfectly, a second station would reveal a curve identical with that of the first station. The assumption is consistent with the theoretical case of a circular stream and a homogeneous community. Most of the data discussed in this paper are based on curve-analysis of single curves.

In Figure 3 the oxygen curve, rate-of-change curve, and resulting component curves of respiration and diffusion are shown for the River Lark based on data given by Butcher, Pentelow, and Woodley (1930). It should be emphasized that this single-curve procedure is no substitute for a double-curve analysis, but is useful in obtaining orders of magnitude. A partial curve analysis was used by Jackson and McFadden (1954) for measuring production in a lake.

Spot method

A very simple method used by the author and J. Yount for obtaining upstream-downstream changes in flowing water is outlined as follows: A spot of fluorescein dye is placed

in the water and followed for about 15 minutes. Measurements are taken in water adjacent to the marker spot before and after the period. Then the observers return upstream to the starting point before making the second measurement. In this way a diurnal rate of change curve is obtained which is then analyzed to obtain diffusion, respiration, and production as described above. This method was used for a bed of marine turtle grass (*Thalassia*) in 3 ft of water along the causeway at Long Key, Florida (Table 2). This is probably the simplest of all the methods described here.

PRODUCTION AND COMMUNITY STRUCTURE OF STREAM COMMUNITIES

Magnitudes of primary production in streams

Using the methods described in preceding sections, data from the literature have been used to obtain the estimates in Table 2. For comparison recall that eutrophic lakes have a gross primary production of organic matter of the order of magnitude of 1 (0.5-5) g/m²/day (Gessner 1949) during seasons of maximum growth; oceanic waters have gross production magnitudes of 0.17-1.6 g/m²/day (Riley 1953); terrestrial agriculture under the best circumstances achieves sustained net production of 10-20 g/m²/day (Kalle 1948); and mass *Chlorella*-cultures under strong light and bubbling carbon-dioxide yield a net production of 2-19 g/m²/day (Wassink, Kok, and Oorschot 1953). If the ratio of photosynthesis to respiration is about 2.0 this indicates a maximum gross primary production of *Chlorella* of 28 g/m²/day. It is immediately observed that the estimates in Table 2 for production in flowing waters are very high. It may be suggested that streams are among the most productive biological environments, a conclusion that has been suspected for a long time on the basis of estimates of standing crop.

Comparison among the streams indicates that the highest primary production rates are in the recovery zones of streams polluted with organic wastes. Thus the pollution not only increases the biota due to an additional organic nutritive source, but subse-

TABLE 2. Productivity and classification of flowing water communities on the basis of oxygen metabolism data

Stream, Date, Source	P Gross production g/m ² /day	R Community respiration g/m ² /day	P/R	K Gas transfer coefficient g/m ² /hr at % saturation
Autotrophic communities ($P/R > 1$)				
Windward coral reef, Eniwetok, July, 1954 (Odum and Odum 1955)	24	24	1	—
Silver Springs, Florida (Odum) respiration from bell jars				
Winter, 1952, 1953	8	2.8	2.9	—
March 23-24, 1954	35	5	7.0	0.92
Birs, Switzerland (Schmassman 1951) ¹ April 11-12, 1946	50	18	2.8	3.3
White River, Indiana; zone of recovery from pollution (Denham 1938) ¹ July 23-24, 1933	57	18	3.2	1.6
Kljasma, Russia (Brujewica 1931) ¹ July 21, 1929	2.4	1.9	1.3	0.6
10 Florida Springs (Odum) July, August, 1955	0.6-59.	—	>1	—
Turtle Grass, Long Key, Florida (Odum and Yount) August 14, 1955	34.	24.	1.4	2.6
Heterotrophic communities ($P/R < 1$)				
Itchen River, England; unpolluted (Butcher, <i>et al.</i> 1930) ¹ , Figure 4				
April-October	5.5-14.0	5.8-18.6	0.6-1.1	0.9-2.8
November-March	0.4-7.1	4.2-20.2	0.1-0.5	1.5-4.3
River Lark, England; polluted (Butcher <i>et al.</i> 1930) ¹				
November 17-18, 1927	0.53	53	0.01	—
May 18-19, 1927	39.	35	1.1	2.3
White River Indiana, near pollution outfall (Denham 1938) ¹ July 21, 1934	0.24	29	0.008	1.22
Potomac Estuary; balance sheet calculation by Purdy, 1917 (quoted by Phelps 1944), eelgrass; polluted	11.0	16.8	0.66	3.7
San Diego Bay, black bottle method; production estimates of Nusbaum and Miller (1952)	2.8	4.4	0.65	1-2.

¹ Diurnal oxygen curves from the paper cited were used as described in the text to obtain production, respiration, and gas transfer estimates.

quently increases the autotrophic based growth rates.

High production is not limited, however, to polluted waters. Three flows with the lowest organic matter contents of all waters (0.1-1 ppm)—the Pacific coral reef environment, the Caribbean turtle grass and the large artesian calcareous springs in Florida—possess very high productivities (Table 2).

The seasonal course of gross production and community respiration has been calculated for the unpolluted River Itchen from data given by Butcher, Pentelow, and Woodley (1930) and summarized in Figure 4. Each point was obtained with a curve analysis like that in Figure 3. An approximation was introduced in the calculations by the use of the average depth 0.6 m rather than the river stages on the particular days, which were not readily available. The pro-

duction curve shows a seasonal trend correlated with the course of sunlight. That the light is the main cause of this pattern seems likely. A similar curve was found in the constant temperature of Silver Springs (Odum 1954). Verduin (1956) found that naturally adjusted plankton populations had a primary production independent of temperature. The constancy of respiration in Figure 4 is supported by Butcher, Pentelow, and Woodley's (1930) account of fairly constant benthic plant populations during the year in the River Itchen. That similar values of the gas transfer coefficients were obtained (Table 1) in spite of the depth approximation used, gives one some confidence in the single-curve analysis procedure used. The seasonal shift in K values for a given stream may not be more than 2- or 3-fold. Although the downstream longitudinal

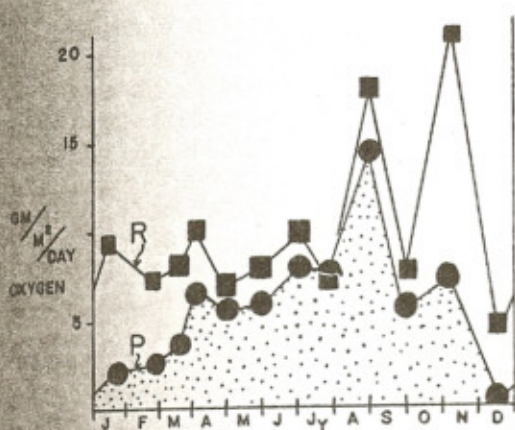


FIG. 4. Seasonal course of production (*P*) and community respiration (*R*) for the Itchen River, England, estimated with the single-station method from data given by Butcher, Pentelow, and Woodley (1930). Production per day in ppm was converted to an areal basis using an approximate depth of 0.6 meters. The stream was unpolluted, calcareous, and contained large plant populations.

succession of species, physical conditions, and rates of waste decomposition are now well-known and fairly similar throughout the world where studied, almost no effort has been made to estimate the primary production rates in the recovery sequence below sewage pollution discharges. Using some oxygen curves of Calvert (1932, 1933) and Denham (1938) for the White River in Indiana, the single-curve procedure has been used to obtain the longitudinal distribution of primary production and respiration over

the 160 miles below the Indianapolis waste outfall. As shown in the pattern in Figure 5, respiratory metabolism far exceeds production in the first 20 miles as the sewage decomposes. Production, however, rises rapidly so that primary production far exceeds the decomposition processes in the early recovery zone. Here the organic matter is being made faster than it is being used. The rise in respiration that seems to occur below this point may be a result of the increased organic matter and increased populations of respiratory organisms. This is in keeping with the idea that the respiratory metabolism of a polluted stream is proportional to the organic matter content at a rate determined by the deoxygenation constant (Streeter 1935, Velz 1939, Phelps 1944). The second peak of respiratory metabolism 100 miles downstream is accompanied by aerobic daytime conditions although the diurnal variation is large. A supersaturated oxygen condition during the day and an anaerobic condition at night is a property of such waters. For example, Schmassmann (1951) used the range of oxygen concentration to classify such streams. Low oxygen and high organic matter are therefore not always correlated. Far downstream there is a gradual decline of both production and respiration. The pattern of maximum primary production in the early recovery zone fits the observed maxima of algal populations in this zone as observed,

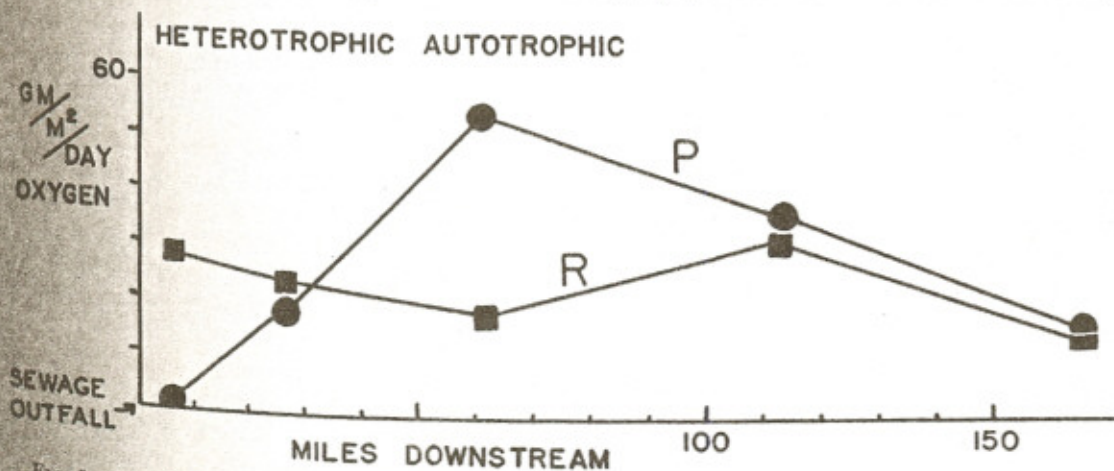


FIG. 5. The downstream sequence of production (*P*) and community respiration (*R*) estimated with the single-station method from data given by Denham (1938) below a sewage pollution outfall in the White River, Indiana, July 21-27, 1934.

for example, in the River Trent by Butcher (quoted by Macan and Worthington 1947).

Enormous values of primary production are also found in recovery zones of other polluted streams as shown in Table 2 and including the River Lark, England, and Birs, Switzerland. It may be found eventually that the most productive communities in existence are those in polluted streams.

Efficiency and current velocity

The estimates of high production in Table 2 for flows of many kinds suggest some consistent difference between the production in running waters and the production in other environments. One is tempted to conclude that the efficiencies of primary production in streams are higher than those of most other environments.

Although many streams maintain higher nutrient concentrations than still waters, this cannot be the entire reason for the high production. The high production-measurements in extremely low nutrient waters at Eniwetok and at Rongelap indicate that nutrient concentration can be overcome where current velocities are large and the organisms are adapted. Ruttner in 1926 (Ruttner 1953) showed that a flow of current past a community accelerates those metabolic processes that are limited by slow rates of diffusion. The current renews the depleted requirements for life and removes accumulating by-products of metabolism. Many organisms adapted to such currents cannot survive outside of the currents. The importance of this phenomenon has been recognized in some small invertebrate animals in their current demand and the high metabolic rates in comparison to similar lake species. Munk and Riley (1952) have made computations as to the effect of falling plankton of various shapes in stimulating their own metabolism by moving relative to the water.

Organic matter, productivity, and succession

In flowing systems there are three time sequences in the adjustment of communities to the physical environment. One is the sequence at one place in the stream, the temporal (short term) succession. The

second is the action of a community upstream in determining subsequent events downstream by affecting the contents of the water passing downstream (the longitudinal succession). The third is the long-time geological succession by which erosion transforms "V"-shaped valley headwaters into flood-plain physiography. Long-time geological processes will not be considered further here. Considerable opinion and evidence exists that temporal succession rapidly leads to an aquatic climax (Butcher, 1945, 1949; Shelford and Eddy 1929), which is maintained until the properties of the water-flow change. Similarly, detailed studies have shown sequences of longitudinal succession such as the pollution-recovery sequence already considered, the cooling sequence downstream from hot springs (Seurat 1922, quoted by Hesse, Allee, and Schmidt 1951), or the diversification sequence downstream from cold springs (Sloan 1956). Although data are scarce, some basic considerations of the production processes may help to relate production to successional sequences.

In Figure 6 is given an energy flow diagram for a community composed of the 5 trophic levels: primary producing plants, herbivores, decomposers, carnivores, and top carnivores. The diagram is drawn so as to separate the photosynthetic part of the community from all the respiratory parts of the community including the plant respiration. Following the first law of thermodynamics the rates of influx of both light and organic matter energy sources are equal to the energy outflux of heat and organic matter. According to the second law of thermodynamics, any process that takes place spontaneously involves a heat loss (dispersal) as an entropy tax. From this diagram it should be clear that when subsequently gross production, net production and respiration are used, community values are intended rather than physiological values.

In many stream communities, there is a large influx of imported organic matter. The word export is appropriate for the organic matter that leaves an active community either by being sent downstream or sedimented below the active metabolic level

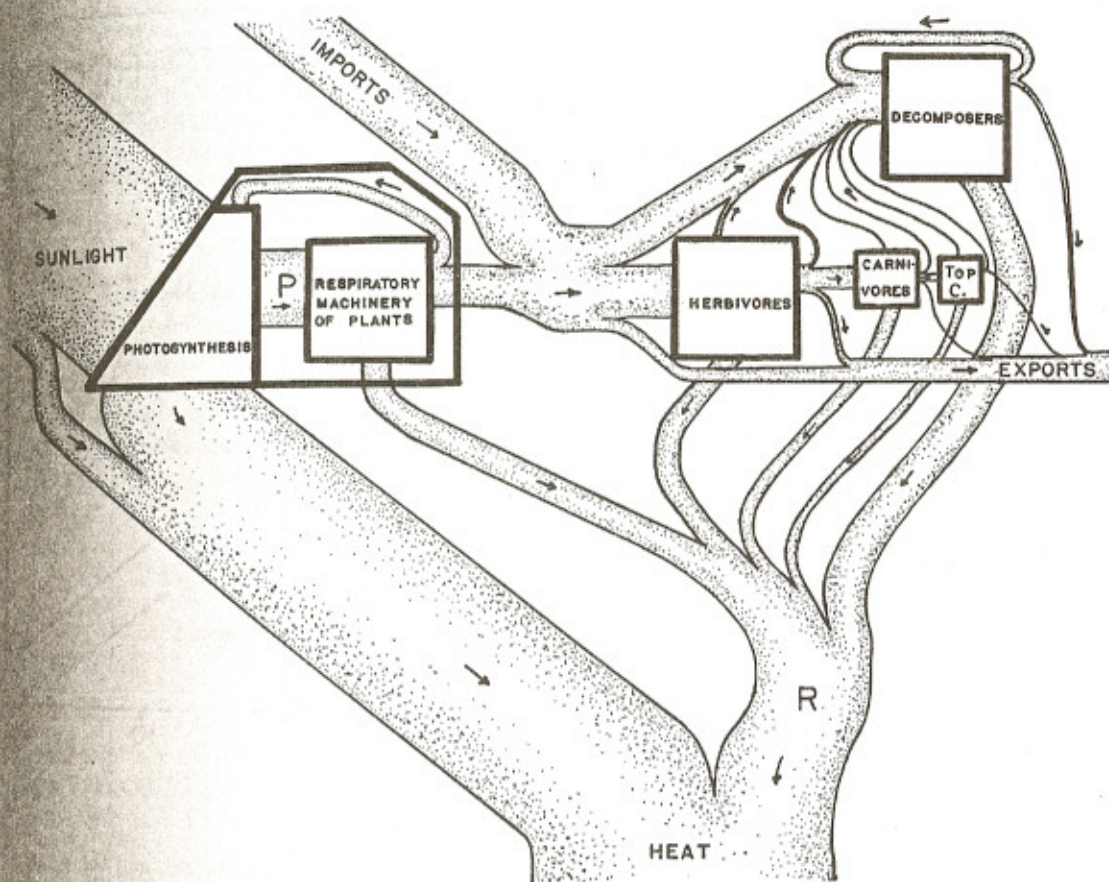


Fig. 6. A generalized diagram of energy flow for steady-state natural communities. P is the gross primary production; R is the total community respiration; the 5 trophic levels are indicated by boxes. Imports and exports are included as dominant flows which may equal the flow of primary production in some streams. The flow from the top of those boxes representing consumer trophic levels indicates unassimilated materials. The laws of thermodynamics are illustrated since inflows balance outflows and every process is accompanied by dispersion of heat energy as entropy tax.

(into a condition of low oxidation potential) of the community. Thus for the whole flowing community:

$$I_m + P = E_x + R \quad (9)$$

where I_m is the import rate, E_x the export rate, P the production rate, and R the community respiration rate. The quantity of consumers that can be supported is dependent both on the primary production and the import.

There seems to be inherent in these arrangements a self-regulating mechanism that tends to direct longitudinal succession but not succession *in situ*. If as cited above for polluted streams, the respiration is a function of the concentration of organic matter

in the water and on the bottom, while the primary production is a function of light and nutrients, there is possible an organic matter concentration in the water at which production will balance respiration. For concentrations of organic matter below this there will be too little available free energy in organic matter to build large populations of organisms. In these cases production will exceed respiration and there will be a net storage or export of organic matter. On the other hand when respiration exceeds production there will be a net loss or import of organic matter. The types of standing crop characteristic of these regions may show dramatic differences. Silver Springs, Florida, is an example of a community that has

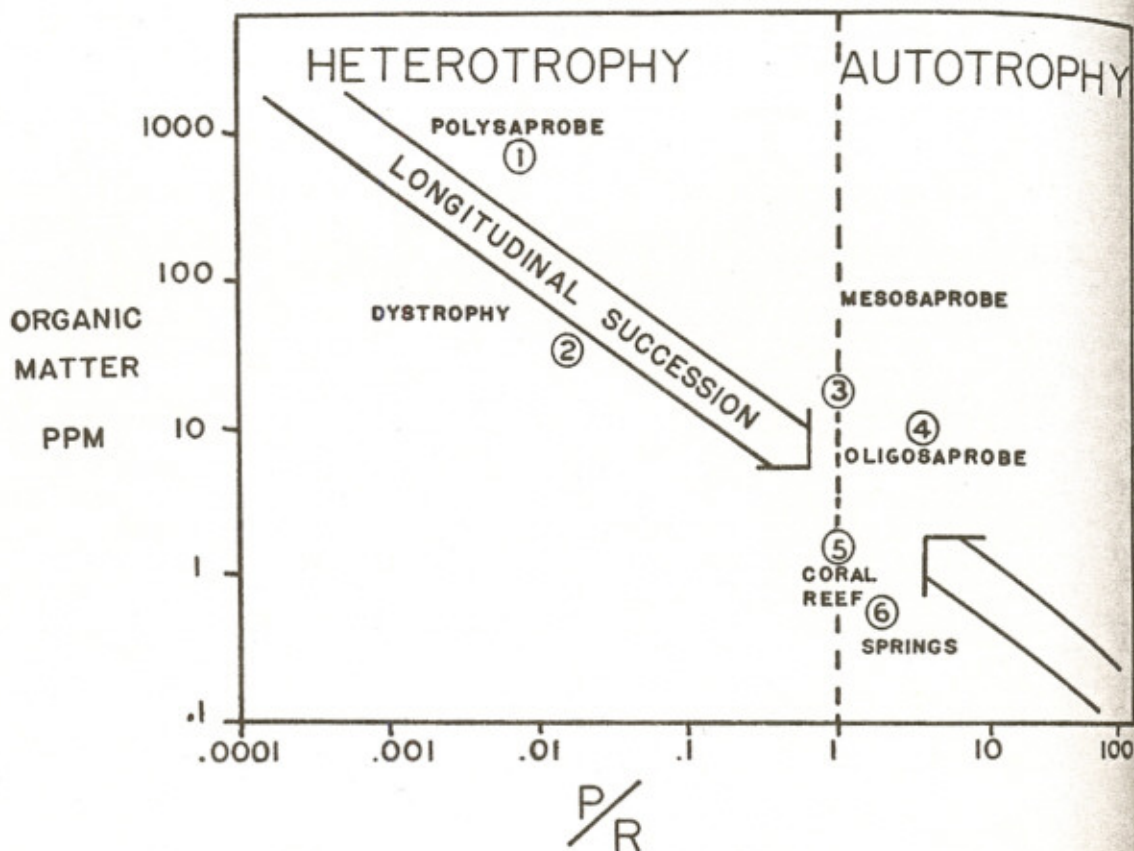


FIG. 7. The relationship of longitudinal succession, total organic matter in waters, and the relative dominance of autotrophic and heterotrophic metabolism as indicated by the P/R ratio. The arrows indicate the trend of concentration of organic matter in waters, depending on the P/R ratio of the communities over which the water flows. Several specific communities are plotted: (1) White River pollution outfall (see Fig. 5); (2) an approximate point for a dystrophic stream based on the observation that the oxygen tension remains below saturation (3.5 ppm) both day and night (Santa Fe River, Fla., Oct. 31, 1953); (3) recovery zone of the Illinois River at Averyville, Aug. 24, 1927, from single station calculation of diurnal oxygen curve given by Mohlman *et al.* (1931); (4) Birs, Switzerland (Table 2); (5) coral reefs from Sargent and Austin (1948, 1954), and Rongelap and Eniwetok from Odum and Odum (1955); (6) Silver Springs, Fla., annual means.

an excess of production over respiration so that the organic matter is exported and the particulate organic content of the water increases downstream. Thus longitudinal succession beginning with either high or low organic content will trend towards an intermediate organic matter content as a steady state downstream condition. Within the length of most streams there is not time for much succession. Many streams with large and continual allochthonous organic matter imports from land drainage will be in an arrested longitudinal succession. These concepts can be made operational if the ratio of production to respiration can be related to

the concentration of organic matter in the water (expressed in mg/l). For natural summer light intensities the organic matter content corresponding to a P/R of 1 is of the order of magnitude of 1–15 ppm. Purdy (1935) found photosynthesis exceeded respiration in mixed algal and bacterial cultures containing 10 ppm dextrose and peptone. Many harmonic and unpolluted lakes and oceans tend to be maintained in this range (Thunmark 1937, Birge and Juday 1926). According to this thinking, deviations much below or above this range cannot occur without addition and removal of organic matter by other agencies, as in

ground water filtration or in allochthonous organic matter drainages. These trends are summarized in Figure 7.

Temporal succession in one place in flowing systems is unable to modify its own water environment, since its products are whisked away to cause downstream succession. Thus successional phenomena in streams are much more a function of the

influx than in terrestrial or still water communities. It seems likely that there are a great many possible climaxes depending on the hydrographic climate provided by the inflowing water. A rational basis for classifying these climaxes in terms of production and respiration processes is provided by the P/R ratio.

The tendency for the P/R values to ap-

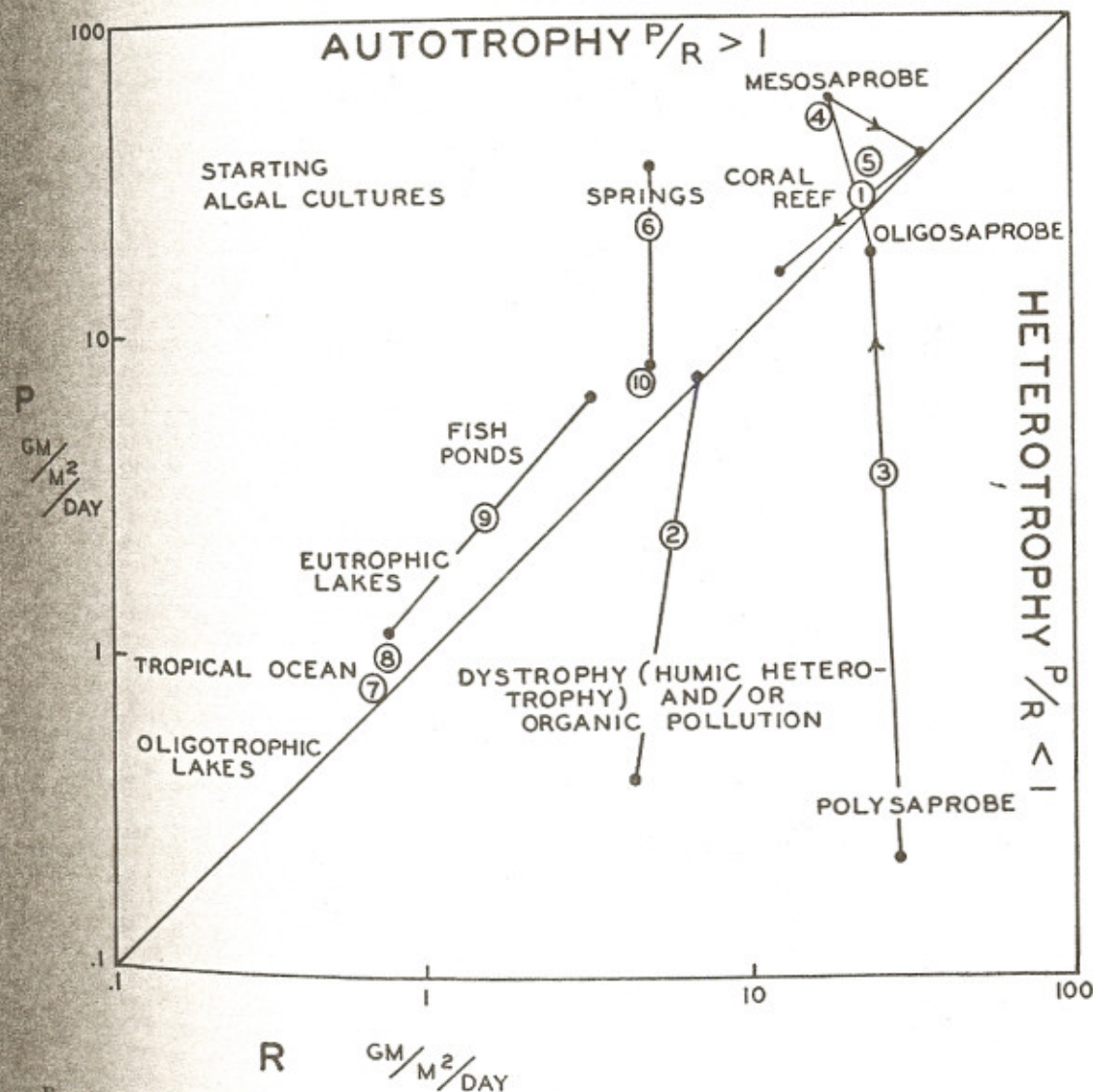


Fig. 8. A diagram for the functional classification of communities according to the total metabolism and relative dominance of autotrophic and heterotrophic metabolism. Specific examples are indicated as follows: (1) Coral reefs (Table 2); (2) Itchen River, England (Fig. 4 and Table 2); (3) recovery sequence on the White River, Indiana (see Figure 5); (4) Birs, Switzerland (see Table 2); (5) Turtle grass (see Table 2); (6) Silver Springs (see Table 2); (7) Tropical ocean (after Riley 1953); (8) Linsley Pond, Conn. (Riley 1940); (9) Little John Pond, Wisconsin (Juday, Blair, and Wilda 1943); (10) fish ponds (from Winberg, 1937, as quoted by Juday *et al.* 1943). Ryther (1954) described the behavior of the P/R ratio in algal cultures.

proach some moderate value is consistent with the qualitative description of rocky stream biota, which is dominated by algae in the headwaters and by consumer animals in the downstream sections. Pennak (1943) described a dominance of phytoplankton over zooplankton in the headwaters of a mountain stream. An amusing example was provided by Nikolsky (1937), who showed that fishes in the headwaters of the Amudaria River had gut lengths 235% of body length, decreasing to but only 170% of body length in the delta. The long guts are presumably a correlation of the plant-eating habits of the fish in the headwaters.

The P/R diagram

As described in the foregoing paragraphs the P/R ratio enables one to make a logical classification of communities into autotrophic and heterotrophic types. In Figure 8, P and R are used as coordinates of a diagram thus providing a useful graph for quantitative comparison of communities. The flowing water communities discussed in this paper are plotted along with some representative values from other environments. The diagram shows how some streams may be fertile in having high total respiratory metabolism and yet possess little primary productivity. It may be desirable to distinguish heterotrophic and autotrophic types of fertility with such terms as heterotrophic, hetero-oligotrophic, auto-eutrophic, and auto-oligotrophic. The diagram suggests a quantitative definition of dystrophy as a term applicable to communities with humic-colored water and a P/R less than 1.

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